

Synonymy of *Homalopoltys* (Araneae: Araneidae) with the genus *Dolichognatha* (Araneae: Tetragnathidae) and descriptions of two new species

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Abstract

Through discovery of their males, females described as *Homalopoltys* Simon (Araneidae) are found to be congeneric with *Dolichognatha* O.P.-Cambridge (Tetragnathidae). Some of the character states seen in *Homalopoltys* (type species *H. incanescens* Simon) do not fit within the current diagnosis of *Dolichognatha* so the potential transfer is tested using the data matrix of Hormiga *et al.* (1995). It is found that the synonymy of *Homalopoltys* with *Dolichognatha* is justified according to current terms of reference. Both described *Homalopoltys* species were known only from Sri Lanka. The male of *D. incanescens* (Simon) (NEW COMBINATION) is described for the first time, and the range of this species is extended to north-eastern Australia. *Dolichognatha albida* (Simon) (NEW COMBINATION) is redescribed and new material is reported from Thailand but the species is still known only from females. *Dolichognatha mandibularis* (Thorell), with similar morphology to *D. incanescens*, is also redescribed but is only known from a single male (Sumatra). Two new species are described: *D. deelemanae* sp. nov. is from Kalimantan and *D. raveni* sp. nov. is from north-eastern Australia and New Guinea. The character states that unite the genus *Dolichognatha* are discussed and some potential new character systems are put forward. Some of the fresh specimens of *D. albida* and *D. incanescens* show that reflective tapeta are present in the secondary eyes and the abdominal morphology of these and the newly described species differs from that of other known *Dolichognatha* species.

Key words: Canoe tapetum, Sri Lanka, Borneo, Thailand, Sumatra, New Guinea, Australia

Introduction

The genus *Dolichognatha* O.P.-Cambridge 1869 is widespread, mainly in tropical and sub-tropical areas (Levi 1981; Platnick 2007). *Dolichognatha* have a characteristic appearance, with large prominent anterior median eyes and a distinctively shaped carapace, which often has the sides almost parallel in the caput region and is evenly rounded posteriorly. Males have elongate chelicerae, some spectacularly so to an extent that some authors have attributed species to the Archaeidae (see Forster & Platnick 1984; Levi 1981). All previously recognised species (except *D. mandibularis* (Thorell 1894)) have two pairs of posterodorsal humps on the abdomen, and Levi (1981) reported that reflective tapeta are absent from all the secondary eyes. *Dolichognatha* species construct horizontal or sloping orb webs.

Levi (1981) synonymised five genera with *Dolichognatha*: *Landana* Simon 1883, *Paraebius* Thorell 1894, *Prolochus* Thorell 1895, *Nicholasia* Bryant & Archer 1940, and *Afiamalu* Marples 1955. One of these synonymies, that of *Paraebius*, was considered uncertain by Levi due to the lack of abdominal tubercles and the arrangement of cheliceral teeth in the holotype male—the only known specimen. Whilst trying to identify the male of *Homalopoltys* Simon 1895 for a study of the tribe Poltyini (Smith 2005), it was noticed that the male type of *Paraebius*, *D. mandibularis*, had certain features in common with the female types of both species of *Homalopoltys* (based on notes and drawings of H. Levi). The females of *Homalopoltys albidus* Simon

1895 have an anteriorly attenuated abdomen, but no abdominal humps as such, whereas females of *H. incanescens* Simon 1895, the type species of *Homalopolrys*, have a bilobed abdomen. Simon placed *Homalopolrys* in the tribe Poltyini, in his family Argiopinae, due to a perceived similarity with *Polrys* C.L. Koch 1843. A sub-adult male *Polrys* specimen shares the vial with the *H. albida* type and this cue may have caused Simon to overlook the otherwise distinctive carapace shape of a *Dolichognatha*. Instead he noted the abdominal shape that is reminiscent of some *Polrys* species that Simon was familiar with. The type locality of *Dolichognatha mandibularis* is Sumatra; both species of *Homalopolrys* were described from Sri Lanka. The new specimens (males and females) are from Sri Lanka, Borneo, Thailand, New Guinea and Australia.

This paper transfers the genus *Homalopolrys* from the Araneidae into the Tetragnathidae and synonymises *Homalopolrys* with *Dolichognatha*. Three existing species are redescribed, *D. mandibularis*, *D. incanescens* and *D. albida* and two new species are described, *D. deelemanae* sp. nov. from Borneo, with an abdominal shape similar to *D. albida*, and *D. raveni* sp. nov. from Australia and New Guinea, which is most similar to *D. incanescens*.

Material and methods

Specimen preparation and examination

Most specimen examinations, measurements and drawings of larger parts were made using a Wild M5 microscope or an Olympus SZ16 stereo microscope, both fitted with measurement graticule and camera lucida. An Olympus BH-2 compound microscope was also used for some genitalia examinations. Male palpal organs and female genitalia were examined whilst suspended in a drop of water-soluble glycerine-based gel mounted on a glass slide using the method of Coddington (1983). The figured expanded male palpus was prepared by repeated transfer between a weak potassium hydroxide solution and distilled water, then mounting as described above. Half-tone drawings were made on coarse-grade coquille board using graphite pencils and an ink outline. Genitalia were drawn in ink on drafting film from enlarged original pencil drawings. All plates were made up using Adobe® Photoshop® 5.0 LE. Lateral views are of the left side unless indicated. Habitus lateral views are composite—one specimen, but parts drawn separately and composed on tracing paper. In these habitus drawings the point of leg excision is representational; leg I has been manipulated so that a flat lateral view is shown to illustrate the proportion to the carapace; leg II femur length is in correct proportion to leg I; legs III and IV are drawn as seen. Specimen preparations for scanning electron microscopy were cleaned ultrasonically before being one of: directly air dried (legs, chelicerae), taken through 80–100% alcohol stages and air dried from 100% acetone (spinnerets), or critical point dried in a microporous capsule after passing through an alcohol series (male palp). All measurements are in millimetres. Carapace length for measured specimens is followed by a range value in parentheses. Eye measurements are across the lens seen in profile; eye separation measurements are lens margin–lens margin at the closest point, also in profile. Eye measurements are approximate due to the difficulty of getting a clear view of certain specimens without dismemberment.

Phylogenetic analysis

The character states of the three taxa detailed in this study for which both sexes are known were scored in accordance with Hormiga *et al.* (1995) (Table 1). In general any character requiring SEM is only resolved for *H. incanescens*, the best represented species. Refer to Hormiga *et al.* for full character list and codings for other species. Here, the scoring of three characters requires some comment:

Character 2 (chelicerae stridulatory striae, males). Not examined under SEM; the scored absence is based on the apparent texture of the relevant part of the cuticle, which is similar to other areas of the cheliceral surface.

Character 3 (lateral eyes of the male separate or touching). The eyes are extremely closely spaced in most of these newly added taxa but point in different directions and there is a small but distinct gap between the edges of the lenses in all three species.

Character 8 (patella–tibia autospasy). Specimens were only tested (by gently pulling on one or more legs, as suggested in Hormiga *et al.*) for species represented by many specimens or by subadults.

The character matrix (Hormiga *et al.* 1995 plus new taxa) was run using TNT (Goloboff *et al.* 2003–2007), using implicit enumeration (Hendy & Penny 1982) which ensures all shortest length trees are discovered. The resulting tree files were imported into Winclada (Nixon 1999–2002) and a consensus tree was printed.

TABLE 1. Coding for the three new taxa represented by both sexes. For character definitions and full data set see Hormiga *et al.* (1995).

nsp_dele	000??01??0?0001??0100100101011000001?000?????????????????????
Homa_inca	0001101000?00010-01001001010110000011000?????????????0010100
nsp_rav	000??01??0?0001??0100100101011000001?000?????????????????????

Abbreviations

The following abbreviations for morphological features are used in the text and figures:

ac	aciniform spigot(s);
agg	aggregate spigot(s);
ALE	anterior lateral eye(s);
ALS	anterior lateral spinneret(s);
AME	anterior median eye(s);
BH	basal haematodocha;
CBP	cymbial basal process;
CD	copulatory duct;
Co	conductor;
cyl	cylindrical spigot(s);
Cym	cymbium;
E	embolus;
F	flange;
FD	fertilisation duct;
fl	flagelliform spigot;
I, II, III, IV	Roman numerals used in reference to legs 1–4;
LS	labral spur;
mAP	minor ampullate spigot;
MAP	major ampullate spigot;
MEA	‘metine’ embolic apophysis (<i>sensu</i> Hormiga <i>et al.</i> 1995);
Pc	paracymbium;
PGM	post genital mound;
pir	piriform spigot(s);

PLE	posterior lateral eye(s);
PLS	posterior lateral spinneret(s);
PME	posterior median eye(s);
PMS	posterior median spinneret(s);
SEM	scanning electron microscopy or microscope;
Sp	spermatheca;
ST	sub-tegulum;
T	tegulum;
TO	tarsal organ.

The following abbreviations are used for repository institutions:

AM	Australian Museum, Sydney, Australia;
BMNH	The Natural History Museum, London, UK;
CLD	C.L. Deeleman-Reinhold (to become part of RMNH coll.);
MNHNP	Muséum National d'Histoire Naturelle, Paris, France;
NHRM	Swedish Museum of Natural History, Stockholm, Sweden;
OUM	Oxford University Museum, Oxford, UK;
QM	Queensland Museum, Brisbane, Australia;
RBIN	Royal Belgian Institute of Natural Sciences, Brussels, Belgium;
RMNH	National Museum of Natural History, Leiden, The Netherlands.

Results

Implicit enumeration of the data using TNT took just over 20 minutes and recovered two minimal-length trees of 132 steps. The two trees are topologically as found by Hormiga *et al.* (1995) except in one the placement of *Azilia* Keyserling 1881 is sister to the clade containing the true metines and tetragnathines, rather than as the sister of the new *Dolichognatha* clade. In both trees the newly added taxa collapse to a polytomy with, or at the base of, the previously included *Dolichognatha* species; this arrangement is preserved by a strict consensus (Fig. 72; unambiguous optimisation shown). The only characters that separate the previously included *Dolichognatha* species are the characters coding presence/absence of tapeta in the posterior eyes (chars 4 and 5); however these characters are now suspected to be variable among species already included in the genus (see Discussion, below). The clustering of the three newly added taxa with the representative taxon of *Dolichognatha* chosen by Hormiga *et al.* (1995) supports the inclusion of *Homalopolrys* in *Dolichognatha*, and thus also supports Levi's (1981) tentative synonymy of *Paraebius mandibularis*, which is morphologically similar to *D. incanescens*.

The newly enlarged genus *Dolichognatha* is still unambiguously supported by four of the five autapomorphies found by Hormiga *et al.* (1995): male versus female cheliceral size larger (char. 15), palpal patellar macroseta absent (char. 19), paracymbium secondary process procurved (char. 25) and metine embolic apophysis present (char. 37). The additional autapomorphy of legs flexed at the web hub (char. 42) is still shown under fast optimisation (ACCTRAN), but has not been scored for any of the newly added taxa.

Despite the unambiguous results found, these autapomorphies are unlikely to provide a comprehensive diagnosis for the genus *Dolichognatha* and several further character systems that might prove informative are discussed below. The assimilation of *Homalopolrys*, with some character states that are new in respect to previous diagnoses, also invites further research into intrageneric structure in *Dolichognatha*. The original data matrix of Hormiga *et al.* used here was not designed to resolve intrageneric relationships, thus it is no surprise that resolution is lacking at this level. In addition, there are many missing entries for the less well represented species, and in the behavioural section for all the newly added taxa.

Discussion

The cladogram presented by Hormiga *et al.* (1995: fig. 30) showed four unambiguous and one ambiguous character optimisations as autapomorphies for the genus *Dolichognatha*. A further 3 unambiguous optimisations (all eye characters) supported the clade of *Dolichognatha* + *Azilia*. The newly added taxa agree with the previously found autapomorphies (entries are missing for the ambiguous behavioural character 42), and these character states may well prove to be diagnostic. Yet there is considerable structural diversity amongst the taxa now included within *Dolichognatha*, and some species clusters, such as the five species in this paper, should be investigated in future as part of a comprehensive generic revision. The characters chosen by Hormiga *et al.* were appropriate for the level of resolution required by their study, but several others might be useful in the more localised context of the internal structure of *Dolichognatha* and relationships with tetragnathid genera such as *Azilia*. Here, starting with the previously noted autapomorphies, I discuss some of the morphological attributes of the five taxa that are new additions to the genus to provide a starting point for future work.

The first of the four character states that unambiguously support *Dolichognatha* is male versus female cheliceral size. Whilst agreeing in general with this character, the males of the newly added taxa have a cheliceral arrangement that is quite distinctive within the genus and this was one of the characters that concerned Levi (1981) about *D. mandibularis*. Most *Dolichognatha* species have the cheliceral teeth confined to the distal part of the paturon but in the newly added taxa and *D. mandibularis* the cheliceral teeth extend up to between one third and one half of the paturon length (e.g. Fig. 61). In these taxa the tooth rows become indistinct after two or three large promarginal and three or four small to medium retromarginal teeth. Where the tooth rows converge there is a medium or large intermediate tooth (Figs. 42, 61) plus an additional small tooth (*D. deelemanae*) or blunt mound (other species, Fig. 61, arrowed) near the position of the fang tip. The fangs (Fig. 42) are long and slightly sinuous. In these taxa male cheliceral characters have not been used for specific diagnoses because there is insufficient material available to adequately assess the variation (see Levi 1981 for discussion of this variation in *Tetragnatha* Latreille 1804), but once known they may prove useful. The chelicerae of females are similar to or shorter than those of other *Dolichognatha* species (Figs 20, 46); the cheliceral boss is smooth and not well developed (Fig. 11). Female chelicerae bear two distinct promarginal teeth plus a large intermediate where the rows meet (Figs 9, 10, intermediate tooth arrowed); one large and about 4 small retromarginal teeth are grouped distally (Fig. 10, 23).

The other character states that unambiguously support *Dolichognatha* are concerned with the male palpal appendage, which in general is quite conservative in morphology throughout the genus. The absence of palpal patellar macrosetae does not require further comment in this context but the shape of the sclerites scored for the other characters is quite stable among the newly added taxa and *D. mandibularis* compared to some other *Dolichognatha* species. The paracymbial secondary process, now termed cymbial basal process (Kuntner & Alvarez-Padilla 2006), is U-shaped in these taxa (Fig. 14: CBP, but note the dorsal procurved hook appears to have become tucked-in on the SEM specimen: it is usually more prominent, as in the mesal view of Fig. 38 (arrowed)) and the paracymbium is a tall, pro-ventral prominence (Fig. 14). The metine embolic apophysis (MEA) is a thick, fleshy strap (Figs 13, 14), often broadened distally. In some *Dolichognatha* species it narrows to a point, e.g. *D. pentagona* (Hentz 1850), *D. ducke* Lise 1993 (Levi 1981 figs 13–15; Lise 1993 fig. 17), in others it is rather similar to the present species, e.g. *Dolichognatha* sp. ex Peru (Hormiga *et al.* 1995 fig. 13B).

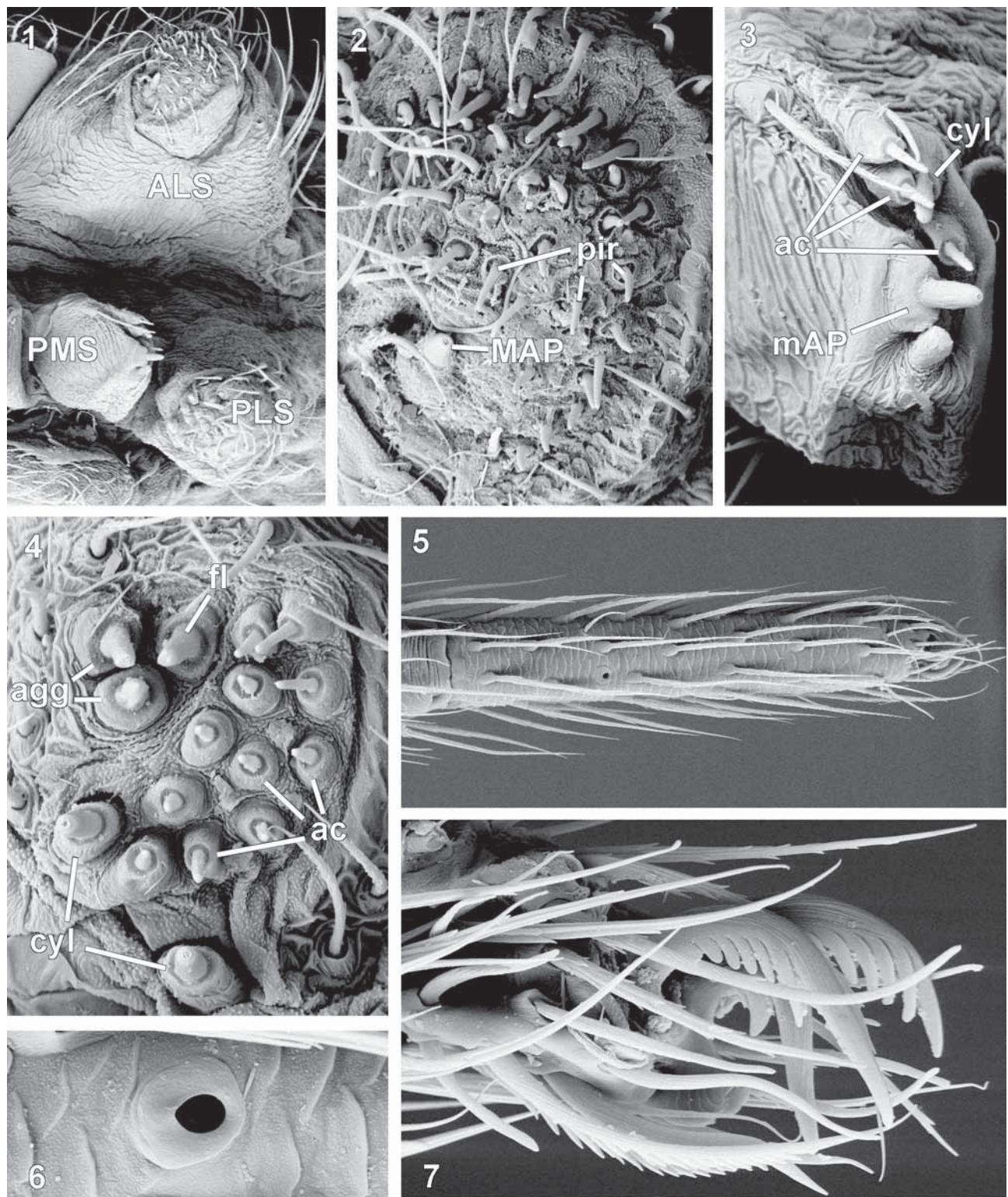
The ocular characters that formerly united *Dolichognatha* with *Azilia* in a clade may prove informative in future work. The *Dolichognatha* species scored by Hormiga *et al.* (1995) had separated lateral eyes in the male (char. 3). This is in agreement with the diagnoses of *Dolichognatha* given by Levi (1981) and Tanikawa (1991). The species described by Lise (1993), however, as well as many of those described by Brescovit and Cunha (2001), are reported to have touching lateral eyes. In the newly added taxa the lateral eyes are closely spaced (e.g. Fig. 62) except in *D. deelemanae* (Fig. 29) but the lenses never touch. The eyes point in different directions and are clearly on separate tubercles in *D. deelemanae*, but this is indeterminable in the other taxa.

The presence of the reflective tapetum in the former *Homalopoltys* species in both PME and PLE is probably the main factor unsettling the relationship between *Dolichognatha* and *Azilia* in this current analysis (chars 4 and 5). Well preserved female specimens show a reflective canoe-shaped tapetum in all secondary eyes (all seen clearly only in *D. incanescens* at January 2007); males are less clear, with a reflective tapetum seen faintly in ALE and PME of the described male of *D. incanescens* only. It seems likely, however, that the tapetal characters have been overlooked previously in some taxa already included in *Dolichognatha* s.l.. The original information on tapetal structure and the absence of a reflective layer was given by Levi (1981) and absence was included in the generic diagnosis given by Tanikawa (1991); these diagnoses are in reference to *Dolichognatha* s.str. or to old specimens. Hormiga *et al.* (1995) scored reflective tapeta as absent for the taxa examined in the original study, at least one of which was *Dolichognatha* s.str. Neither Lise (1993) nor Brescovit & Cunha (2001) commented on this character. In the present study no reflective tapetum was visible in any of the examined *Dolichognatha* s.str. specimens, although several were collected relatively recently and are in comparable, or better, condition than the *D. incanescens* in which this character was particularly evident at the time of writing. Nevertheless, recently collected male specimens of *Dolichognatha* s.l. from Sulawesi (BMNH) with elongate and distally modified chelicerae were observed, in 2006, to have clearly visible reflective tapeta in the posterior median eyes (PME). Further, *Dolichognatha* females from Kalimantan (RMNH ex CLD) which appear to have ovoid abdomens, without humps, have reflective tapeta clearly visible in all secondary eyes. All the additional specimens examined as part of this study are listed in the Appendix.

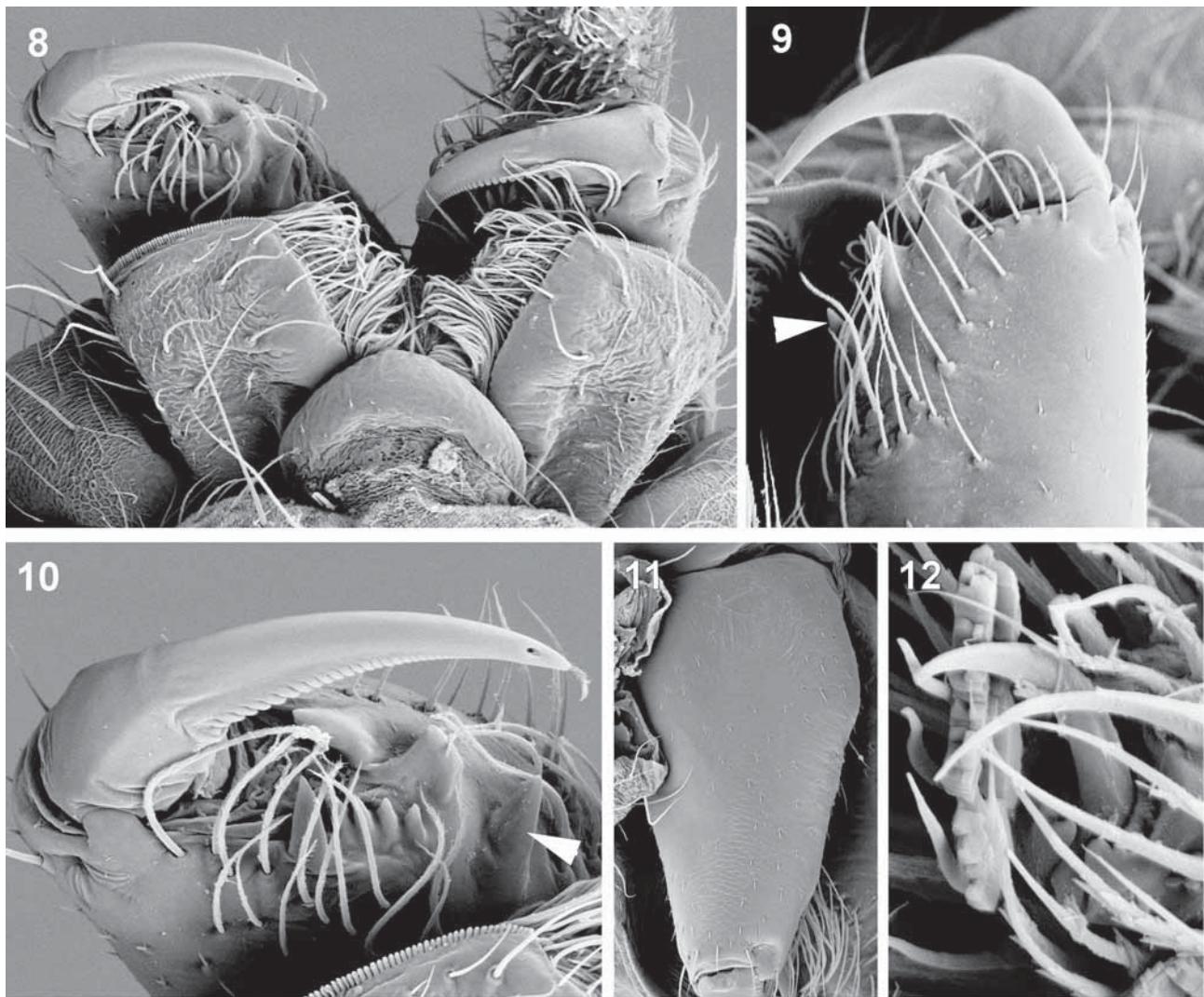
Some new characters that may prove useful have previously been figured for one or more *Dolichognatha* taxa, but their distribution is unknown through the genus and related taxa. These include a labral spur in males, the number and arrangement of spinneret spigots, and details of the morphology of the genitalia. The labral spur, found in the males of all of the newly added taxa (Figs 29, 38) is presently reported in *D. maturaca* Lise 1993 (Lise 1993: figs 3, 5; Brescovit & Cunha 2001: fig. 4) and is also present in *Dolichognatha* sp. ex Fiji (see Appendix). Lise (1993) reported that the spur was absent in the other *Dolichognatha* species described in the same paper, *D. ducke*. Except for illustrating the labral spur of *D. maturaca* using SEM, Brescovit & Cunha (2001) do not discuss this feature in respect to other species described in their paper. Examination of spinneret spigots in *Dolichognatha* has been carried out only for *D. pentagona* (Hormiga *et al.* 1995: fig. 24) and now also *D. incanescens* (Figs 1–4). The similarity between the two taxa is striking, with only minor differences in the numbers of piriform spigots on the ALS and aciniforms on the PLS apparent (both slightly more numerous in *D. incanescens*, Figs 2, 4). The spinneret characters used by Hormiga *et al.* (1995) were fairly broadly defined, but this close similarity between related taxa might indicate that useful fine scale generic differences could become apparent with a more comprehensive sample of taxa.

Interesting structures and similarities are also revealed by detailed comparisons between male palpal structures (Figs 13, 45, 65, c.f. Brescovit & Cunha 2001: fig. 7; Hormiga *et al.* 1995: fig. 13 B, C). A scanning electron microscope reveals that the cymbial tarsal organ of *D. incanescens* is large (Figs 13, 15) and in a marginal position similar to that of *D. maturaca* (Brescovit & Cunha 2001: figs. 7, 8). Despite its apparent size, the tarsal organ is barely distinguishable under a light microscope. Another cymbial character may come from the arc of setae that can be seen on the prolateral margin of the cymbium (Fig. 15). This appears as an indistinct lamina under a light microscope and could be an alternative explanation for the apparently unclear lobe drawn with dotted lines for *D. umbrophila* Tanikawa 1991 (figs 9, 10). This setal arc corresponds with the position of the embolus tip in the unexpanded palp (Fig. 43) and makes the tip difficult to see properly. Another unexplained feature apparently depicted in the illustrated *D. umbrophila* (Tanikawa 1991, fig. 10), but not mentioned in the description, is a retrolateral flange on the cymbium (F in Figs 14, 65). Under a light microscope this is only clearly visible on the larger (QM) *D. raveni* male but its presence is indicated by a refractive margin on smaller specimens. Other palpal structures associated with the embolus may or may not prove to be informative. For instance embolic processes are reported sporadically through the genus, e.g. in *Dolichognatha* ex Peru (Hormiga *et al.* 1995 fig. 13B, C), *D. mapia* Brescovit and Cunha 2001 (figs 24, 25) and *D. maturaca* and *D. ducke* (Lise 1993, figs 12, 17). Amongst the newly added species only *D. raveni*

(arrow Fig. 65) has a similar process. One structure observed in *D. incanescens* is a membranous lamina attached along the embolus in parallel with the free part of conductor (arrow Fig. 45). This has not been investigated in any other taxa.



FIGURES 1–7. *Dolichognatha incanescens* female (RBIN). 1–4, spinnerets. 1, spinneret field, left side. 2, ALS. 3, PMS. 4, PLS (right side, image reversed). 5–7, legs. 5, dorsal tarsus, left leg IV. 6, tarsal organ, left leg I. 7, tarsal claws, left leg I.

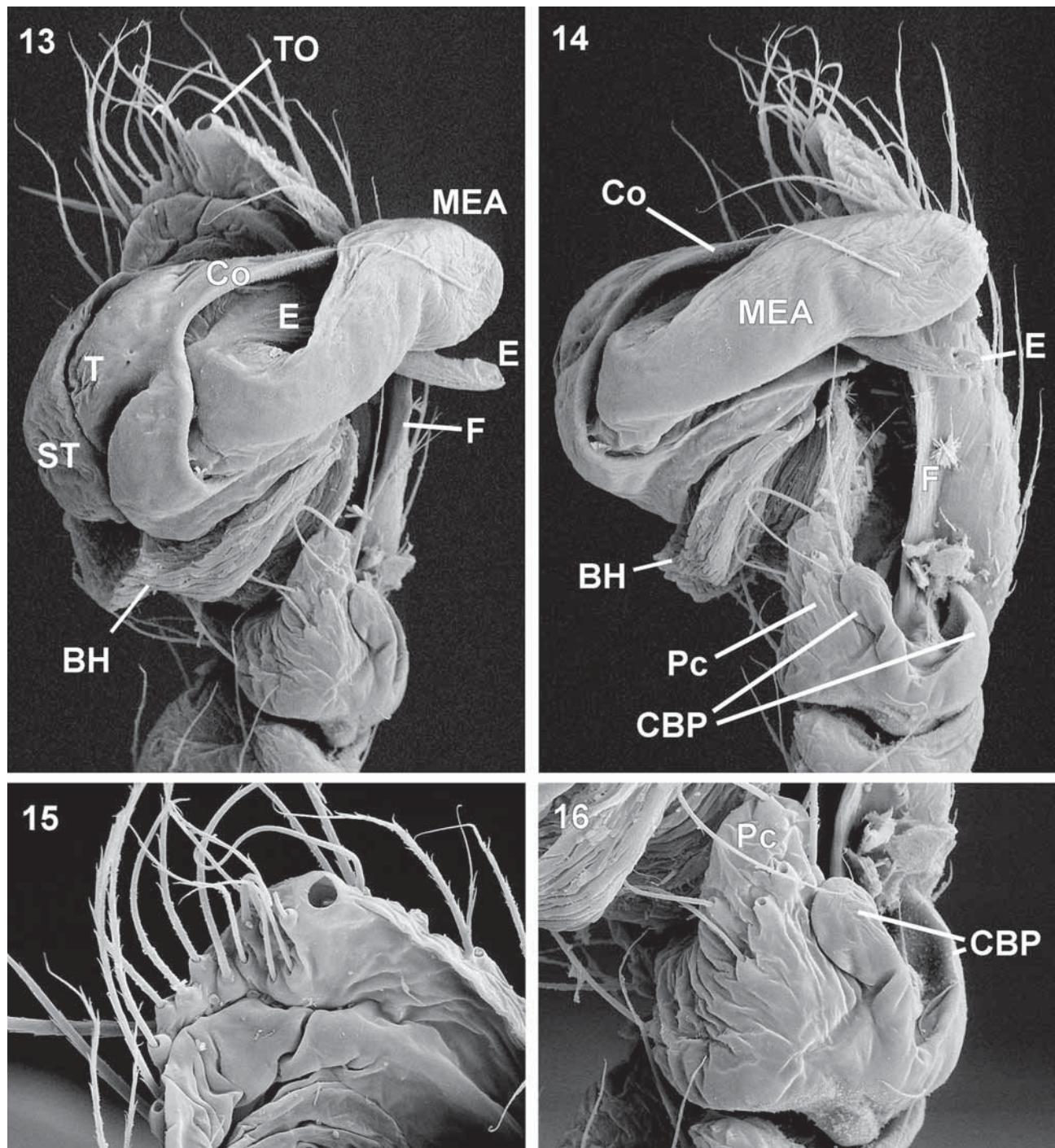


FIGURES 8–12. *Dolichognatha incanescens* female (RBIN). 8–11, mouthparts. 8, labium, maxillae and chelicerae. 9, right chelicera, anterior view, showing promarginal teeth; large intermediate tooth arrowed. 10, right chelicera, posteroventral, showing retromarginal teeth; large intermediate tooth arrowed. 11, right chelicera, lateral. 12, tarsal claw, left palpus.

Another area of potential interest and already used in some Araneae taxa are the claws and sensilla. In *Dolichognatha incanescens* the tarsal claws of leg I have c. 6 flattened teeth on superior claws, two teeth on the inferior claw, one rather small (Fig. 7); toothed accessory hairs are present. On leg IV the superior claws have c. three teeth, sustentaculum is absent. The tarsal organ is a simple ovoid pit (Fig. 6), positioned at approximately 1/3 tarsus length (Fig. 5). The female palpus bears a fine claw without teeth (Fig. 12).

The potential characters in the final set to be discussed may prove more difficult to quantify. They include the enlarged anterior median eyes and the distinctive carapace shape, both of which are characteristic of *Dolichognatha* species as a whole. Other potential sources of information may be found through the observation that the five newly added taxa can be seen to form a morphologically distinct sub-group within the genus *Dolichognatha*, although at present this is not recognised formally by the results of the phylogenetic analysis. The most striking difference between these species and all other described *Dolichognatha* species is in the variation in abdominal shape. This, along with the cheliceral structure, was of concern to Levi (1981) in his synonymy of *Paraebius*, because all other known *Dolichognatha* species have four abdominal tubercles. In *Landana*, one of the genera previously synonymised with *Dolichognatha* by Levi (1981), the males had spec-

tacularly elongate chelicerae and highly modified carapace (some *Landana* species were previously placed in the Archaeidae). Levi commented that these extreme morphologies seemed to intergrade with the more usual forms seen in *Dolichognatha* s.str. and this may be found to be the case with other characters and morphologies discussed here. However, rather more taxa have now been described and some of these difficult to quantify characters may now prove to be more informative when examined together with other new characters, such as tapetal information from fresh specimens.



FIGURES 13–16. *Dolichognatha incanescens* male (QM S74356), left palpal organ (partially expanded). 13, retroventral. 14, retrolateral. 15, tarsal organ and arc of macrosetae. 16, cymbial basal process and paracymbium.

The following are some general morphological features that combine to give the newly added taxa a distinctive appearance. The male carapace is pear-shaped in dorsal view (Figs 40, 58), rather humped (Fig. 38),

and shorter than in most *Dolichognatha* s.str., especially noticeable in the caput region where the caput sides may be strongly divergent posteriorly. In females the caput region may be even less strongly differentiated (Fig. 21). The sternum of both males and females is cordate (Figs 23, 41) but, unlike any *Dolichognatha* s.str. specimen examined, is markedly convex in the smaller species (Figs 17, 29). Around the bulging sternum the coxae of legs I and II are produced bulbously ventrad (Fig. 29). On the legs, the femurs are devoid of macrosetae proximally and ventrally, although numerous ordinary setae are present (Figs 22, 38, 46). The prolaternal faces of femurs I and II may be devoid of setae (Fig. 38) or with one or more mid to distally placed macrosetae (*D. albida*, Fig. 22, *D. deelemanae*). Many other *Dolichognatha* species have numerous, and often stout, femoral macrosetae (e.g. *D. pentagona*, Levi 1981 fig. 10). The abdominal shape of males may be a simple ovoid (*D. mandibularis*, *D. incanescens*, Fig. 39) or similar to females and ‘drip’ shape (*D. deelemanae*, Fig. 31) or square anteriorly (*D. raveni*). Females show some degree of variation in the development of abdominal shape and this may also prove to be the case in males. Males of *D. deelemanae* (Fig. 30, PGM) and females of all species except *D. raveni*, have a post genital mound (Fig. 46), a distinct prominence between the genital fold and the posterior spiracle. The term is used rather than ‘genital tubercle’, which was used by Scharff and Coddington (1997) for a protuberance in the same location found in some gasteracanthines. In the definition of Scharff and Coddington the genital tubercle is a female sexual character and is sclerotized; however at least in *D. deelemanae* the mound occurs in both sexes, and, although pigmented, does not appear to be sclerotized.

As more information becomes available and as more specimens of *Dolichognatha* are examined, revision of this variable genus may become desirable. There is no doubt that *Dolichognatha* species are under-reported, for instance the species illustrated by Hormiga *et al.* (1995) from Peru indicates the presence of more species in South America, whilst the five species treated in this present paper are by no means the only undescribed *Dolichognatha* species in the South-East Asian/Australasian region. Levi (1981) discussed undescribed species from New Guinea, at least two species of unknown status are present in Singapore (D. Court, pers. comm.), and several species of *Dolichognatha* s.str. are represented in Australian museums from New Guinea, Fiji and Australia (AM, QM), including the male and female figured by Davies (1988). Full treatment of these, and other as yet unidentified taxa, will be necessary to allow a comprehensive assessment of the true limits of the genus.

Taxonomy

Family Tetragnathidae Menge 1866

Genus *Dolichognatha* O.P.-Cambridge 1869

Dolichognatha O.P.-Cambridge 1869: 387; type species *D. nietneri* O.P.-Cambridge 1869, by monotypy. Not examined. *Landana* Simon 1884: 185; type species *L. petiti* Simon 1884, by monotypy. Not examined.

Paraebius Thorell 1894: 43; type species *P. mandibularis* Thorell 1894, by monotypy. Examined.

Homalopolys Simon 1895: 893; type species *H. incanescens* Simon 1895, by original designation. Examined. NEW SYNONYMY

Prolochus Thorell 1895: 122; type species *P. longiceps* Thorell 1895, by monotypy. Not examined.

Nicholasia Bryant & Archer 1940: 60; type species *Epeira pentagona* Hentz 1850 by monotypy. Not examined.

Afiamalu Marples 1955: 495; type species *A. richardi* Marples 1955 by monotypy. Not examined.

Update on type repositories listed by Levi (1981). The type of *D. nietneri* is not catalogued in BMNH (J. Beccaloni, pers. comm.), the repository given by Levi (1981). Instead this type is likely to be in OUM where six O.P.-Cambridge specimens are catalogued under this name (J. Hogan, pers. comm.). In addition to the syntype of *Prolochus longiceps* in NHRM (T. Kronestedt, pers. comm.) (stated to be the holotype in Levi 1981) there is a vial of syntype material in BMNH. Syntypes and paratypes of *Afiamalu richardi* are in BMNH (information not given by Levi). Types of both *Homalopolys* species are in MNHN.

Diagnosis. All currently recognised *Dolichognatha* have large anterior median eyes, which are prominent on a slight tubercle (Brescovit & Cunha 2001), a distinctively shaped carapace, with sides often subparallel in the caput region and evenly rounded posteriorly (Levi 1981), and in males, long to very long chelicerae with enlarged cheliceral teeth distally (Levi 1981, Brescovit & Cunha 2001). The male palpal patella is without macrosetae. The male palp has a ‘metine’ embolic apophysis (*sensu* Hormiga *et al.* 1995), a prominent paracymbium and procurved cymbial basal process (secondary process of Hormiga *et al.* 1995; Kuntner & Alvarez-Padilla 2006). The abdomen of *Dolichognatha* s.str. bears two pairs of posterodorsal humps, but the abdominal shape may be otherwise in some *Dolichognatha* s.l., including those described herein. Reflective tapeta are absent from all the secondary eyes of *Dolichognatha* s.str. (Levi 1981; Tanikawa 1991), but again may be present in other *Dolichognatha*.

Biology. Species of *Dolichognatha* make orb webs, which are always horizontal or slope less than 45 degrees to horizontal (Levi 1981, F. Alvarez-Padilla pers. comm.). Levi (1981) reports that all the species he observed made similar webs, which were often “messy”, between buttress roots at the base of large trees in relatively moist, dark forests; the collection data of some further specimens listed in the Appendix agree with this description. Whilst all specimens in this present study were collected in tropical forests, many were taken from foliage and by canopy fogging, a departure from the web position just above the ground suggested by all previous records. In all the collection data for the species treated here there is only one mention of a web: a report of *D. albida* specimens being found in a horizontal sheet web between leaves. Regarding such web structure, Simon (1894: 743) reported that the web of the *D. nietneri* he observed in Ceylon (Sri Lanka) was a horizontal sheet, a claim which was discounted by Levi (1981). David Court (pers. comm.) reports that the webs of a *Dolichognatha* sp. he has observed in Singapore may look like a sheet when damaged; this interpretation, at least for Simon’s specimens, seems likely as the specimens collected by Simon in Sri Lanka are in MNHNP, and are *Dolichognatha* s.str. (from photographs supplied by F. Alvarez-Padilla). The report of a sheet web in *D. albida* therefore requires confirmation.

Levi (1981) reported that *Dolichognatha* may include a line of debris and egg sacs in the web, or hanging nearby. Simon (1894) reported (in translation): “The *D. nietneri* that I have observed from Ceylon lays its egg cocoons in a cylindrical truncated sleeve of thick sticky silk suspended from two divergent lines near its web.” These sources are the only published references to *Dolichognatha* biology I have seen.

Dolichognatha albida (Simon)

Figs 17–28

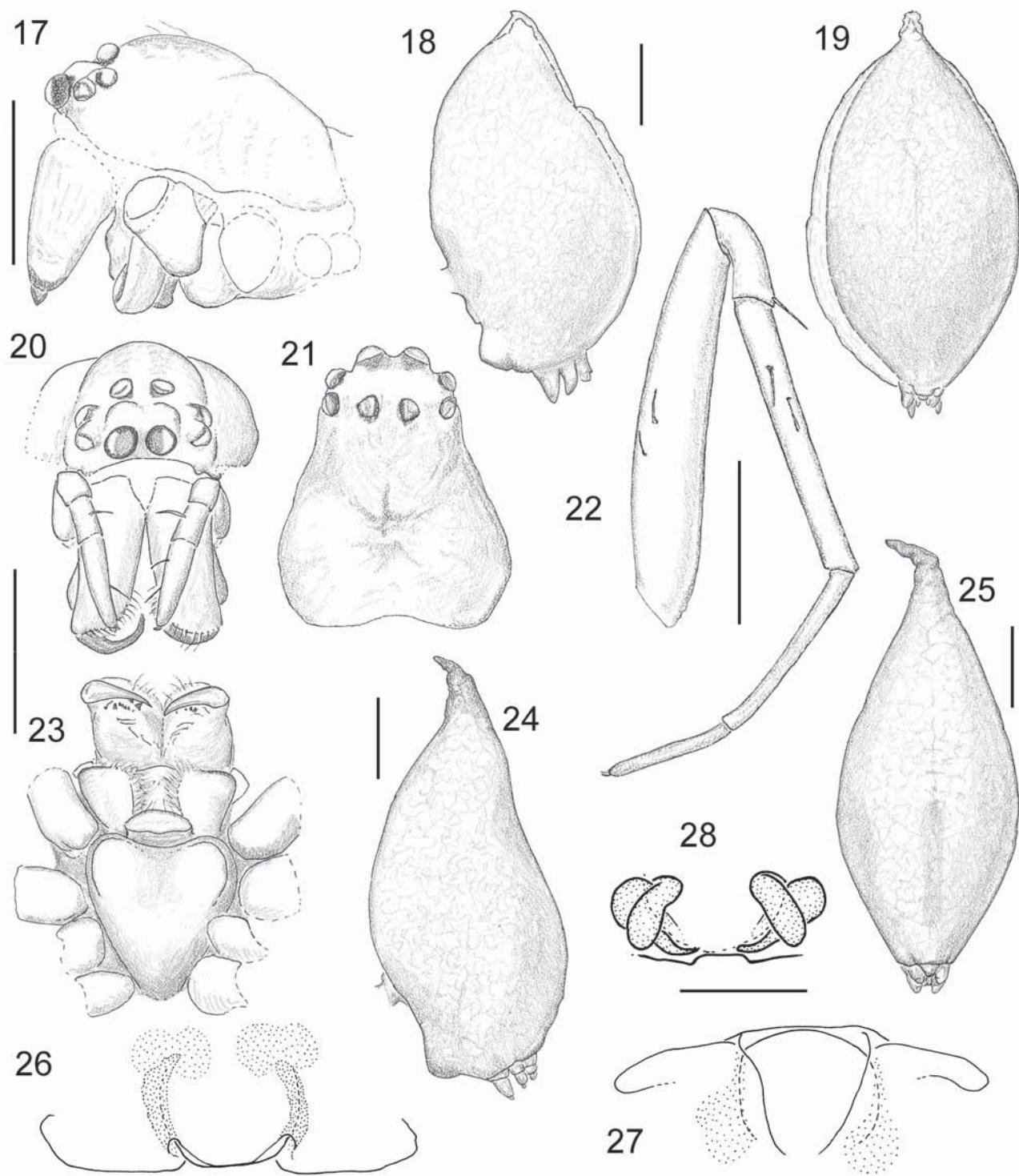
Homalopolys albidus Simon 1895: 894. Holotype ♀, Sri Lanka, Colombo. In MNHNP, No.16281, examined. NEW COMBINATION.

Other material examined. THAILAND: (Central Thailand) 3 ♀, RMNH (ex coll. CLD), Khao Yai National Park, 5.iii.1986, C.L. & P.R. Deeleman, c. 1000 m, in big horizontal web between leaves, no hub; 2 ♂, RMNH (ex coll. CLD), similar location data, ‘near waterfalls’; 1 ♂, RMNH (ex coll. CLD), Erawan Waterfalls National Park, 15–16.iii.1986, C.L. & P.R. Deeleman, evergreen.

Comments. The female from Colombo discussed here is believed to be the type of *H. albidus*, but in the publication the location is given only as “Ins. Taprobane”. For this species there is no contradiction, merely less information than on the specimen label. But in the case of *H. incanescens* (below), where the town locality is in disagreement with the original description, one of the additional specimens present in the *H. albidus* vial provides circumstantial evidence supporting the type status of these *Homalopolys* specimens. This specimen is a subadult male *Polys* C.L. Koch, likely to be the *Polys* ‘male’ from Sri Lanka Simon described in the same paper (1895: 891, fig. 955). Simon’s illustration and his statement that the male lacked a paracymbial

hook (which would have been quite obvious in an adult male *Polrys*, Smith 2005 fig. 10) are indications that the specimen Simon discussed was indeed sub-adult.

Diagnosis. Female. Abdomen apically with 'drip' point (Figs 19, 25); copulatory openings on epigynum set away from posterior margin in ventral view, ducts make a horseshoe shape (Fig. 26).



FIGURES 17–28. *Dolichognatha albida*. 17–23, female (holotype). 17, prosoma, lateral. 18, 19, abdomen lateral, dorsal. 20, part of prosoma, frontal. 21, carapace, dorsal. 22, left leg one showing prolaternal macrosetae. 23, prosoma, ventral. 24, 25, female (RMNH), abdomen lateral, dorsal. 26–28, female epigynum (holotype). 26, ventral. 27, posterior. 28, dorsal (internal genitalia). Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.

Male. Unknown.

Description. Female (holotype). Carapace (Figs 17, 20, 21): length 0.96 (range 0.88–0.98), width 0.73, height 0.55; carapace humped, broadly pear-shaped in dorsal view, caput poorly differentiated in outline but strongly domed. Chelicerae (Figs 17, 23): promargin bears two definite teeth plus large intermediate where rows meet; retromargin bears one large and 4 small teeth grouped distally. Labium: distinctly mounded anteriorly. Sternum (Fig. 23): strongly convex, especially anteriorly. Eyes (Figs 17, 20, 21). AME: 0.10, PME: 0.08, ALE: 0.07, PLE: 0.08, AME–AME: 0.035, AME–ALE: 0.04, PME–PME: 0.04, PME–PLE: 0.06, ALE–PLE: 0.025; no reflective tapeta visible in type specimen, but visible in some females from Thailand. Legs. I: 3.51, II: 3.04, III: 1.73, IV: 2.20; femur I with one strong plus second weaker prolateral macrosetae at mid point (Fig. 22), distal dorsal macroseta missing. Abdomen (Figs 18, 19): length 2.29, width 1.18; anterior bluntly pointed, point more gently attenuated in Thai specimens (Figs 24, 25), tip often wrinkled; post genital mound strongly produced, posterior surface distinctly flattened. Epigynum (Figs 26, 27): copulatory openings set away from posterior margin in ventral view, ducts viewed through cuticle make a horseshoe shape; in posterior view the internal margins of the lateral plates diverge gradually towards copulatory openings. Internal genitalia (Fig. 28): robust copulatory ducts pass anteromedially around spermathecae to enter posterodorsally; spermathecae with globular head, posterior part hidden by copulatory ducts. Colour in alcohol: creamy-white, traces of dark colouring on dorsal carapace and around eyes; dark coloration more extensive on recent specimens, but still lack any sign of leg stripes. Abdomen pale except for darker spot on posterior flat of post-genital mound; recent specimens have traces of pattern dorsally and anterior tip with traces of black.

Distribution. *Dolichognatha albida* is recorded from localities in Thailand and Sri Lanka.

***Dolichognatha deelemanae* sp. n.**

Figs 29–37

Holotype. INDONESIA: Kalimantan: ♂, RMNH.ARA.11299 (ex coll. CLD), SE Kalimantan, Meratus Mtn, E of Lake Riam Kanan, 3.vii.1980, C.L. & P.R. Deeleman, primary forest. **Paratypes.** INDONESIA: Kalimantan: 1 ♂, RMNH.ARA.11300, 1 ♀, RMNH.ARA.11301, data as holotype.

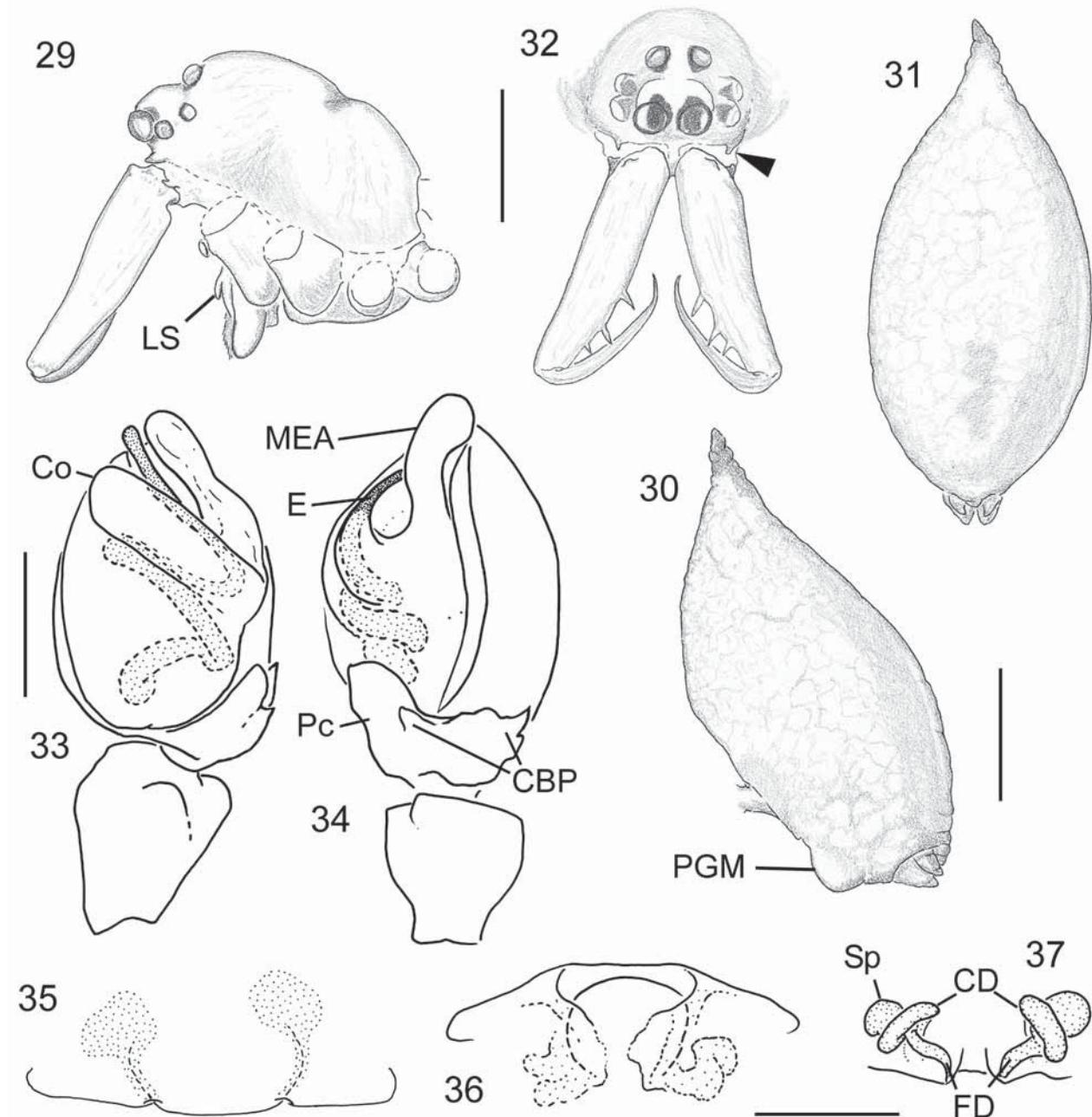
Etymology. The specific epithet honours Christa Deeleman-Reinhold, who collected the specimens which originally sparked interest in this group.

Diagnosis. Male. Palpal bulbus short and rounded (Figs 33, 34), abdomen with apical ‘drip’ point (Fig. 31, may vary), palpal tibia almost as wide as long, MEA broadens only slightly distally.

Female. Abdomen apically with point, copulatory openings of epigynum set almost on posterior margin in ventral view, ducts shorter than in *D. albida* (Fig 35 c.f. Fig. 26), internal genitalia delicate (Fig. 37, c.f. *D. albida*, Fig. 28).

Description. Male (holotype). Carapace (Fig. 29): length 0.78 (range 0.78–0.80), width 0.61, height 0.39; caput strongly humped in lateral view; similar to *D. mandibularis* in dorsal view; caput margins produced to distinct projections anterolaterally over cheliceral bases (arrowed in Fig. 32). Chelicerae (Figs 29, 32): paturon length shorter than in other species (c. 0.8 × carapace length), basal ledge strongly produced, two distinct promarginal cheliceral teeth and one large intermediate, which is the largest tooth, three retromarginal teeth, basal mound absent; cheliceral fangs shorter than other species, and not sinuous, tips arced. Labium: with distinct, but rather recumbent, spur (Fig. 29). Sternum: distinctly convex (Fig. 29). Eyes (Figs 29, 32). AME: 0.10, PME: 0.08, ALE: 0.065, PLE: 0.065, AME–AME: 0.04, AME–ALE: 0.025, PME–PME: 0.04, PME–PLE: 0.06, ALE–PLE: 0.025; no reflective tapeta visible in either male. Legs: I: 3.76, II: 3.12, III: 1.67, IV: 2.24; femur I with strong prolateral macroseta at mid point, femur II with single retrolateral macroseta at c. $\frac{3}{4}$ length; front femurs with at least one distal dorsal macroseta as in other species. Abdomen: length 1.94, width 0.86; apex produced into drip-shaped apex (Fig. 31); post-genital mound strongly developed but without col-

oration (Fig. 30). Palpal organ (Figs 33, 34): palpal femur $0.29 \times$ carapace length; patella without macroseta, tibia short compared to other species, distally almost as wide as long; embolus a curved rod; MEA relatively slender, only slightly broadened distally; overall shape of bulbus similar to *D. mandibularis*, width: length = 1:1.5. Colour in alcohol: almost entirely creamy-white; median eyes with black around margins; faint trace of colour on dorsal carapace.



FIGURES 29–37. *Dolichognatha deelemanae*. 29–34, male (holotype). 29, prosoma, lateral. 30, 31, abdomen lateral, dorsal. 32, carapace and chelicerae, frontal; anterolateral carapace projection arrowed. 33, 34, male palpal organ (holotype), ventral, retrolateral. 35–37, female epigynum (RMNH.ARA.11301). 35, ventral. 36, posterior. 37, dorsal (internal genitalia). Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.

Female (RMNH.ARA.11301). Carapace: length 0.86, width c. 0.55 (slightly squashed), height c. 0.41; caput strongly domed, sides bulging. Chelicerae: promargin with two definite teeth plus large intermediate where rows meet; retromargin with one large and 4 small teeth grouped distally (rather indistinct). Labium:

mounded on anterior face. Sternum: deep, strongly convex. Eyes. AME: 0.10, PME: 0.07, ALE: 0.065, PLE: 0.07, AME-AME: 0.02, AME-ALE: 0.03, PME-PME: 0.04, PME-PLE: 0.065, ALE-PLE: 0.03; no reflective tapeta visible (specimen not in good condition). Legs: I: 3.29, II: 2.94, III: 1.57, IV: 2.12; macrosetae near midpoint of prolateral femur I and 4/5 length of retrolateral femur II. Abdomen: length 1.14, width N/A (squashed); attenuated anterior tip not very well developed, moderately developed post-genital mound. Epigynae: copulatory openings set almost on posterior margin in ventral view, ducts viewed through cuticle short and curved into a flattened bowl shape (Fig. 35); in posterior view the internal margins of the lateral plates diverge sharply towards the copulatory openings (Fig. 36). Internal genitalia (Fig. 37): as *D. albida* but distinctly delicate. Colour in alcohol: creamy-white, traces of dark colouring on dorsal carapace and around eyes. Abdomen pale.

Distribution. *Dolichognatha deelemanae* is only recorded from south-eastern Kalimantan.

***Dolichognatha incanescens* (Simon)**

Figs 1–16, 38–53

Homalopolys incanescens Simon, 1895: 893. Holotype ♀, Sri Lanka, Galle. In MNHNP, No.16311, examined. NEW COMBINATION.

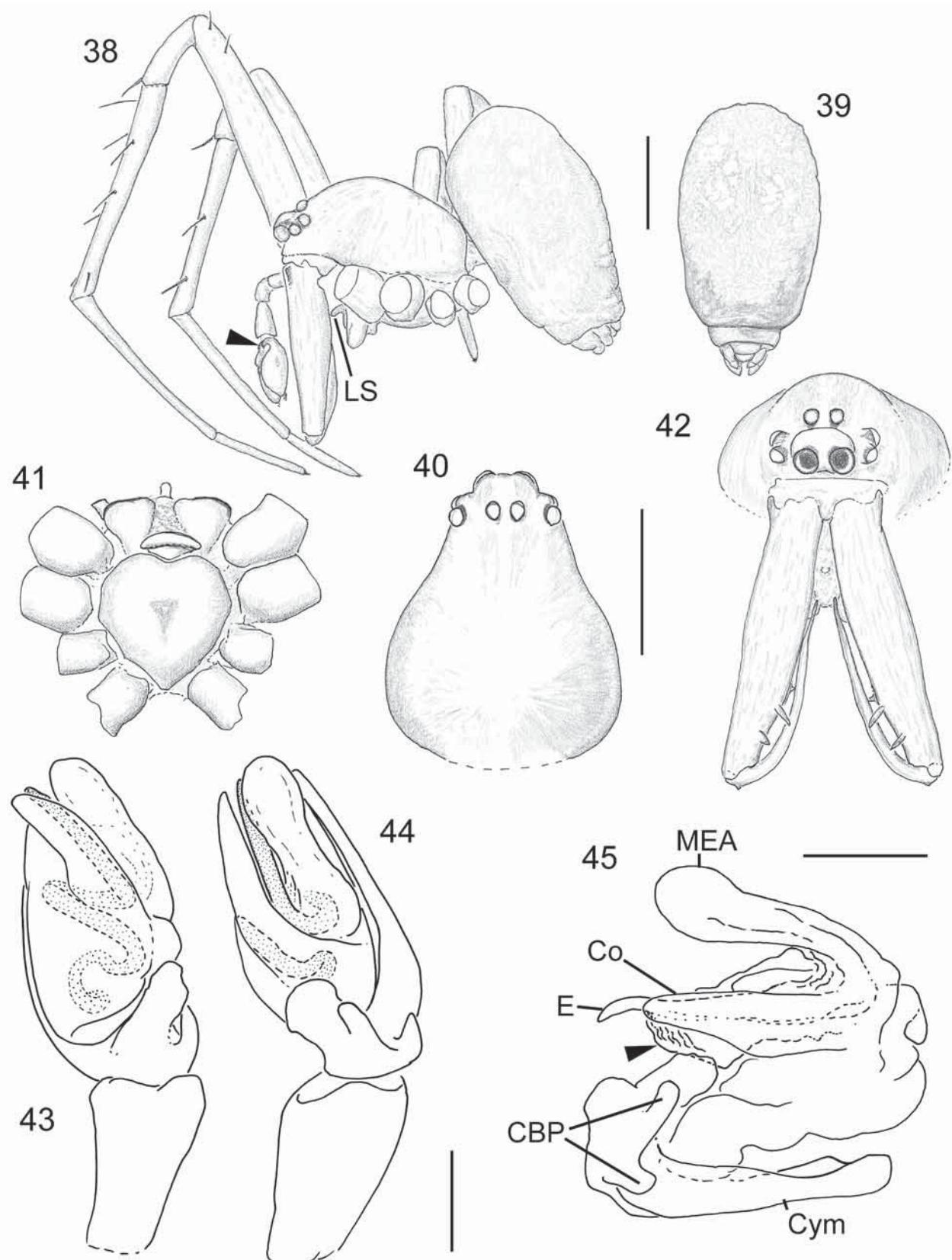
Other material examined. SRI LANKA: ♂, RMNH.ARA.11302 (ex coll. CLD), Ratnapura, 21–22.viii.1981, forest & lake below tennis club. AUSTRALIA: Queensland: 2 ♀, QM S73921, Bellenden Ker Range, Cable-way base stn, 17–24.x.1981, Earthwatch/Qld Museum, 100 m; 2 ♂ 1 ♀, QM S74359, Gordon Creek, Iron Range, 24–30.vi.1976, R. Raven, V.E. Davies; 1 ♂ 1 ♀, AM KS100890, data as S74359; ♂, QM S74358, Spear Creek, 3–10.xi.1975, R. Raven, V.E. Davies; 2 ♂, QM S74356–7, Wallaman Falls, via Ingham, 1.x.1980, G. Monteith, 500 m RF, pyrethrum. PAPUA NEW GUINEA: 4 ♂ 20 ♀, RBIN, Baiteta Forest, 5°01'S 145°45'E, 1993–96, canopy fogging. **Material of doubtful identity:** INDONESIA: Kalimantan: 2 ♀, RMNH (ex coll. CLD), Tumbang Tahai, 2°02'S 113°35'E, 3–11.ix.85, Suh. Djojosudarmo, primary moist forest; ♀, RMNH (ex coll. CLD), Kaharian, 2°02'S 113°40'E, 2–16.ix.85, Suh. Djojosudarmo, swampy primary forest, foliage.

Comments. The female discussed here as the type of *H. incanescens* is believed to be that of E. Simon (1895). As discussed under *D. albida*, the type locality in the specimen vial does not match that given in the original publication, where it is Kandy. There are two registration numbers with the *H. incanescens* specimen. The number used by MNHNP on the loan form is given above. The middle digit on the other label (probably Simon's label, which also carries the locality "Galle !") is not clear, but looks more like a '2'.

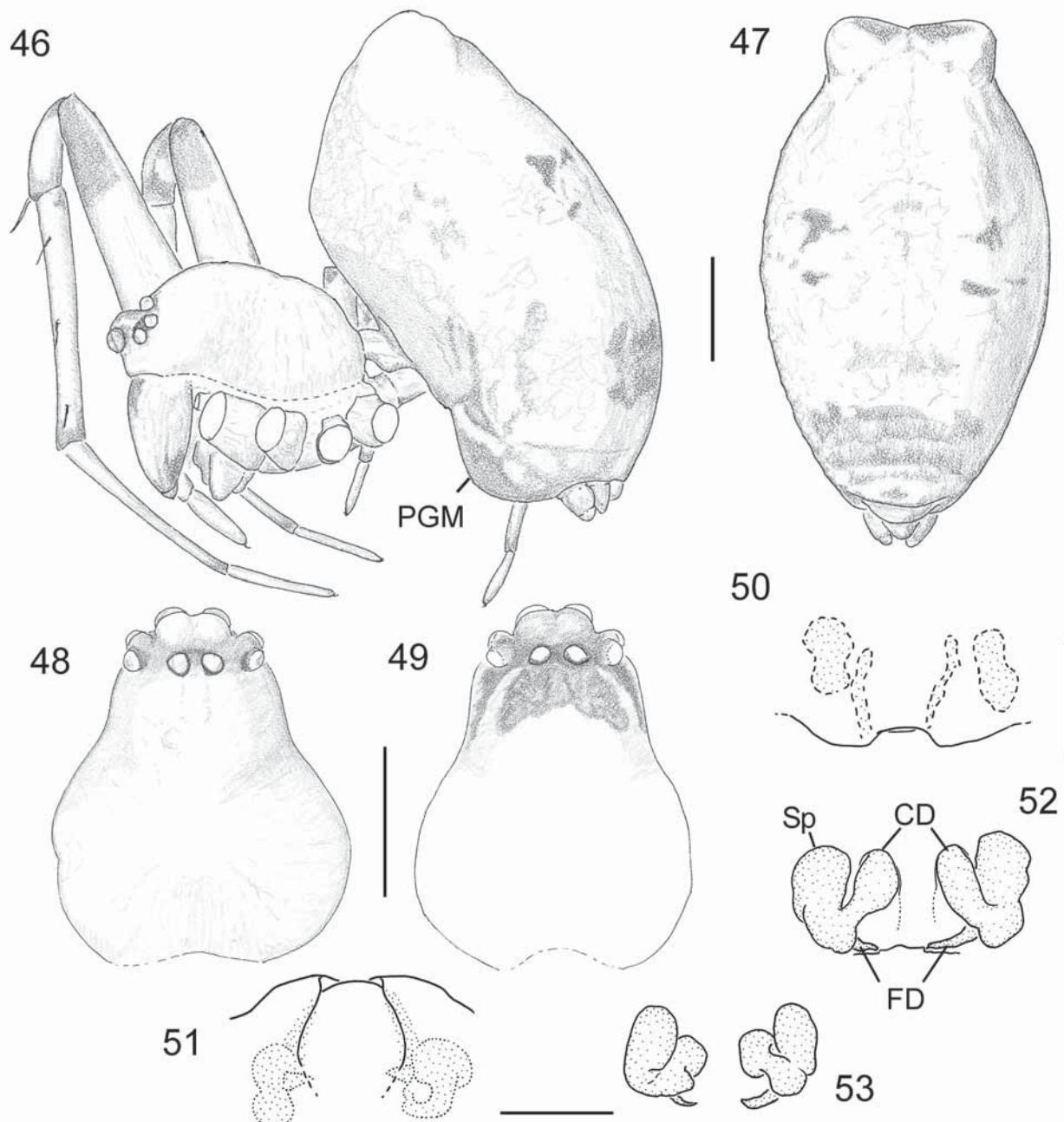
Diagnosis. Male. Palpal bulbus almost twice as long as wide, embolus without spine-like apophysis (Figs 43, 44).

Female. Abdomen bilobed apically in dorsal view (Fig. 47), strongly constricted below apical tubercles; epigynum posterior margin indented medially in ventral view (Fig. 50).

Description. Male (RMNH.ARA.11302). Carapace: length 1.00 (range 0.88–1.08), width 0.82, height 0.55; strongly humped in lateral view (Fig. 38), little differentiation between caput and posterior part (some other males more similar to other species), caput sides sloping in dorsal view (Fig. 40), anterior margins of carapace squared, but with small protrusions in some New Guinea males. Chelicerae (Figs 38, 42): small, angled cheliceral ledge; two distinct promarginal cheliceral teeth, 6 (right) or 5 (left) medium and small teeth scattered intermediately and on retromargin (right side with three small teeth apparently in a transverse row across groove), other males equally variable, one appears to have 5 retromargin teeth on one side but none at all on the other. Labium: labial spur strongly produced (Fig. 38). Sternum (Figs 38, 41): slightly convex, but less so than in *D. deelemanae*. Eyes (Figs 38, 40, 42). AME: 0.10, PME: 0.06, ALE: 0.075, PLE: 0.065, AME-AME: 0.03, AME-ALE: 0.035, PME-PME: 0.03, PME-PLE: 0.07, ALE-PLE: 0.01; outline of tapeta



FIGURES 38–45. *Dolichognatha incanescens* male (RMNH.ARA.11302). 38, lateral habitus; prominent cymbial basal process arrowed. 39, dorsal abdomen. 40, carapace, dorsal. 41, sternum and endites, ventral. 42, carapace and chelicerae, frontal. 43, 44, male palpal organ, ventral, retrolateral. 45, male palpal organ, expanded (RBIN); embolic lamina arrowed. Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.



FIGURES 46–53. *Dolichognatha incanescens* female. 46–48, (holotype). 46, lateral habitus. 47, abdomen, dorsal. 48, carapace, dorsal. 49, female (RBIN), carapace, dorsal. 50–52, female epigynum (holotype). 50, ventral. 51, posterior. 52, dorsal (internal genitalia). 53, *D. incanescens*? (RMNH ex Kalimantan), internal genitalia. Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.

clearly visible in secondary eyes. Legs (Fig 38): I: 4.75, II: 4.04, III: 2.10, IV: 2.53; anterior femurs with three dorsolateral macrosetae distally, 2 prodorsal, 1 retrodorsal. Abdomen (Figs 38, 39): length 1.45, width 0.76; apex rounded; post-genital mound not developed. Palpal organ (Figs 13–16, 43–45): palpal femur $0.29 \times$ carapace length; patella without macroseta, tibia c. 2× as long as wide; embolus gently tapering to blunt tip, embolic apophysis spoon-shaped distally, stem longer and more strap-like than *D. mandibularis*; conductor, embolus and apophysis all more elongate than in *D. mandibularis*; bulbus width: length = 1:1.8. Colour in alcohol: almost entirely pale creamy white and semi translucent in parts; PME with black around margins; faint trace of inverted arrow-head on sternum (Fig. 41); dorsal abdomen with traces of dark pigment posteriorly.

Female (holotype). Carapace: length 1.25 (range 1.00–1.25), width 1.02, height 0.63; in lateral view rather similar to male with caput poorly differentiated from posterior (Fig. 46), rather broad posteriorly in dorsal view, caput region short (Fig. 48); some other females are more similar in carapace shape to other species. Chelicerae: promargin with two definite teeth plus large intermediate where rows meet (Figs 9, 10, intermediate arrowed), retromargin with one large and 4 small teeth grouped distally (Fig. 10). Labium: rounded (Fig. 8), mounded on anterior face. Maxillae with serrula (Fig. 8). Sternum: convex, but less pronounced than in *D. deelemanae*. Eyes (Figs 46, 48): AME: 0.11, PME: 0.09, ALE: 0.09, PLE: 0.08, AME–AME: 0.035, AME–ALE: 0.05, PME–PME: 0.03, PME–PLE: 0.06, ALE–PLE: 0.015; no reflective tapeta present in type, but visible in all secondary eyes of several recently collected females from New Guinea and Queensland; lateral eyes are close in all specimens, but eye position varies both vertically and horizontally. Legs (Fig. 46): I: 4.75, II: 4.20, III: 2.22, IV: 2.78; distal macrosetae missing, no indication of any prolateral macrosetal bases. Abdomen (Figs 46, 47): length 2.53, width 1.39; apically rather more constricted than *D. raveni*, and many New Guinea specimens are narrower still; post genital mound well developed as a rounded bulge, but less distinct in some other specimens. Epigyne (Figs 50, 51): posterior margin broadly indented, copulatory openings hidden in ventral view; in posterior view the internal margins of the lateral plates converge towards the copulatory openings. Internal genitalia (Fig. 52): copulatory ducts pass spermathecae medially, entering posteromedially into lower lobe of spermatheca; spermatheca head globular-ovate. Colour in alcohol: carapace creamy-white, eye region and chelicerae with olive markings, sternum with dark mark. Legs cream with olive-brown annulations, incomplete on femora. Abdomen dorsum pale except for brown patch anterior to anal tubercle and remains of paired markings towards anterior; brown lateral patches; ventrally with olive-brown over post-genital mound, outlined with white lines. The New Guinea females consistently have a slightly different carapace pattern with more brown or black on the caput (Fig. 49) and the brown bar anterior to the spinnerets on the dorsal abdomen becomes black laterally, persisting as black spots in nearly every specimen. The Queensland females are either bleached or in poor condition, but appear to more closely match the holotype colour pattern.

Specimens of doubtful identity. The female specimens examined from Kalimantan have rather shorter copulatory ducts (Fig. 53), no male is available from this area.

Distribution. *Dolichognatha incanescens* occurs from Sri Lanka to north-eastern Australia.

Dolichognatha mandibularis (Thorell)

Figs 54–60

Paraebius mandibularis Thorell 1894: 44. Holotype ♂, Sumatra, Lampung. In NHRM, examined.

Dolichognatha m. Levi 1981: 277.

Comment. It was initially thought that the male of *D. mandibularis* (from Sumatra) might pair with *D. albida* (from Sri Lanka and Thailand) as the short and broad palpal conformation is closest to that of *D. deelemanae*. However, in general appearance the male *D. mandibularis* (Figs 54–58) is more similar to males of *D. incanescens* and *D. raveni*, with a relatively low carapace, similar eye characteristics, and apparently, no macroseta on the prolateral face of the anterior femora. More specimens are required to resolve this issue and for the time being both species are recognised.

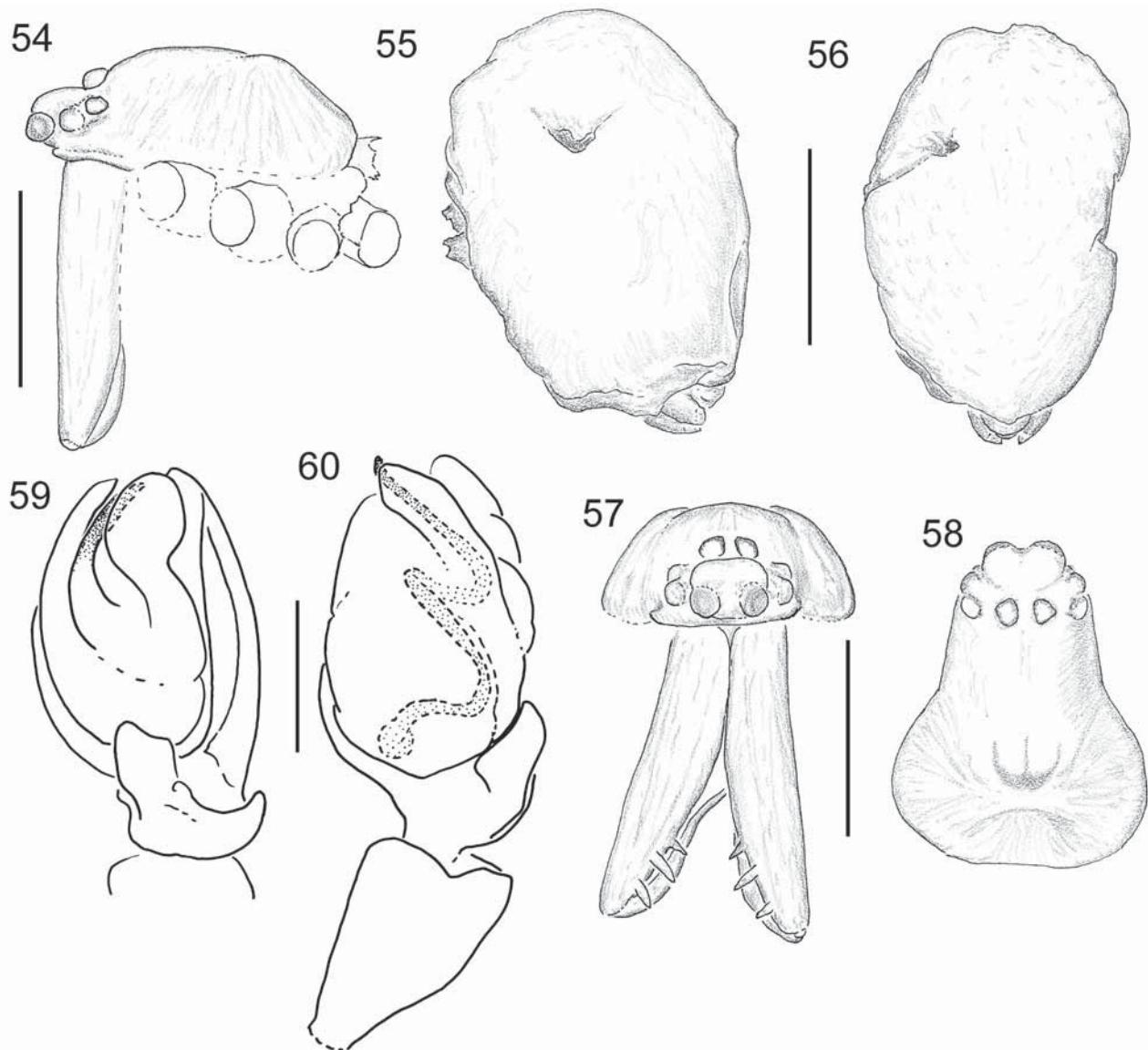
Diagnosis. Male. Palpal bulbus short and rounded, palpal tibia distinctly longer than wide, MEA broad distally (Figs 59, 60).

Female. Unknown.

Description. Male (holotype). Carapace (Figs 54, 57, 58): length 0.86, width 0.67, height 0.29; caput not strongly humped, pear-shaped in dorsal view with caput clearly differentiated. Chelicerae (Fig. 54, 57): cheliceral ledge absent or chelicerae may be pushed up so ledge hidden by carapace; two distinct promarginal cheliceral teeth and one large intermediate, three smaller retromarginal teeth plus basal mound. Labium: with

anterior hooked spur. Sternum: concave (but indented by damage). Eyes (Figs 54, 57, 58). AME: 0.10, PME: 0.075, ALE: 0.075, PLE: 0.06, AME-AME: 0.02, AME-ALE: 0.04, PME-PME: 0.02, PME-PLE: 0.04, ALE-PLE: 0.01; no reflective tapeta visible. Legs. I: 3.57, II: 3.06, III: 1.63, IV: 1.94; almost all macrosetae missing, no indication of any prolateral macrosetal bases. Abdomen (Figs 55, 56): length 1.14, width 0.59; apex rounded; post-genital mound indistinct (holotype abdomen is separate from opisthosoma and rather damaged). Male palpus: (Figs 59, 60): palpal femur 0.27× carapace length; patella without macroseta, tibia c. 2× as long as wide; embolus tapering; MEA squat, strongly spoon-shaped distally; conductor, embolus and apophysis all more compact than in *D. incanescens*; bulbus short and rounded, width: length = 1:1.5. Colour in alcohol: almost entirely creamy-white and in parts semi translucent; PME with hint of black around margins; faint trace of trident-shaped mark on dorsal carapace (Fig. 58).

Distribution. *Dolichognatha mandibularis* is recorded only from the type locality in Sumatra.



FIGURES 54–60. *Dolichognatha mandibularis* male (holotype). 54, prosoma, lateral. 55, 56, abdomen lateral, dorsal. 57, carapace and chelicerae, frontal. 58, carapace, dorsal. 59, 60, male palpal organ, ventral, retrolateral. Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.

***Dolichognatha raveni* sp. n.**

Figs 61–71

Holotype. AUSTRALIA: Queensland: ♀, QM S78040, Gordon Creek, Iron Range, 24–30.vi.1976, R. Raven, V.E. Davies. **Paratypes.** AUSTRALIA: Queensland: ♂, QM S78041, ♀, QM S78042, data as holotype. PAPUA NEW GUINEA: 1♂, RBIN, Baiteta Forest, 5°01'S 145°45'E, 6.iv.1993, canopy fogging, *Pometia pinnata*.

Etymology. The specific epithet is in honour of Robert Raven, who was most helpful in locating the Queensland Museum specimens.

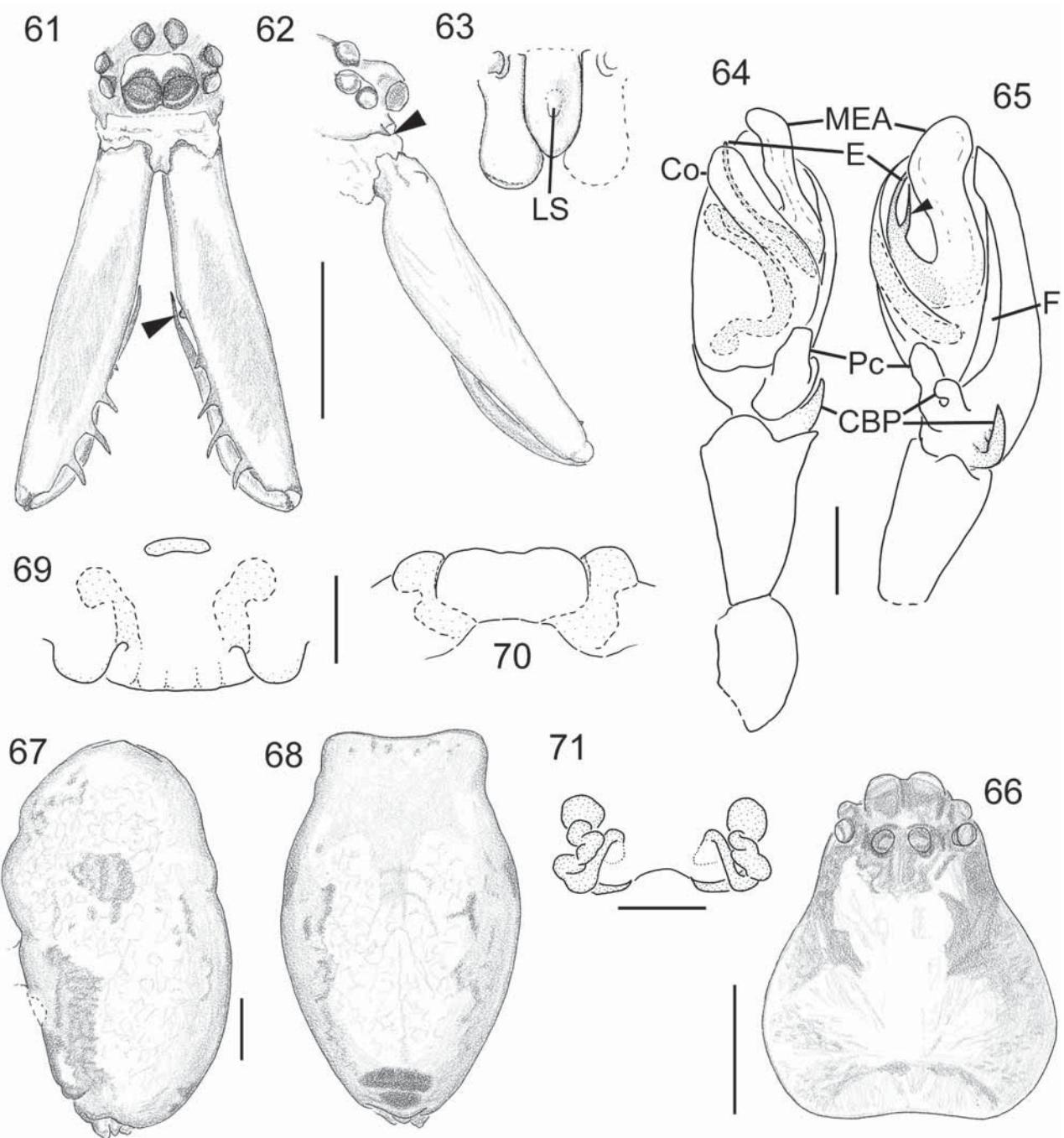
Diagnosis. Male. Palpal bulbus twice as long as wide, embolus with spine-like apophysis (Figs 64–65, apophysis arrowed).

Female. Abdomen broadly bilobed apically (Fig. 68), copulatory openings of epigynum set away from posterior margin in ventral view, epigynum medially broad with marginal sculpturing (Fig. 69).

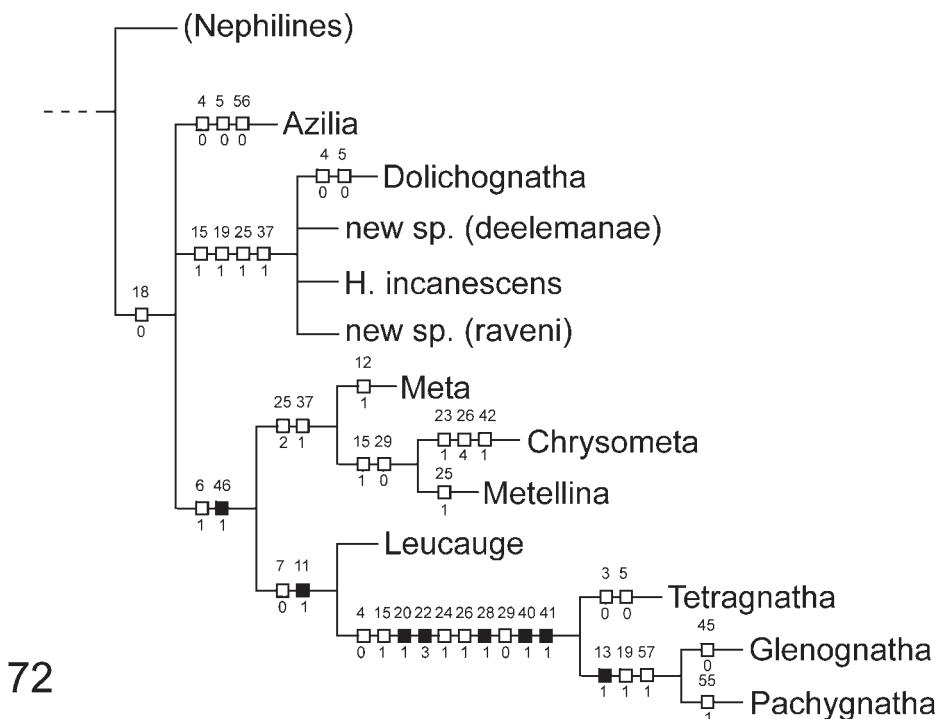
Description. Male (RBIN but QM S78041 figured). Carapace: length 1.07 (range 1.07–1.13), width 0.80, height 0.50; carapace shape similar to *D. mandibularis*, humped but relatively low, in dorsal view caput slightly longer than other species and sides gently diverging; caput margins produced to distinct projections anterolaterally over cheliceral bases (Fig. 62, arrowed). Chelicerae (Figs 61, 62): anterobasal ledge of paturons weak, broadly rounded; three distinct promarginal cheliceral teeth, plus large tooth at convergence of rows, 2 medium and small teeth retromarginally, distinct blunt tooth or mound near fang tip (arrowed in Fig. 61). Labium: labral spur present (Fig. 63). Sternum: slightly convex. Eyes (Figs 61, 62). AME: 0.115, PME: 0.08, ALE: 0.08, PLE: 0.06, AME–AME: 0.02, AME–ALE: 0.02, PME–PME: 0.035, PME–PLE: 0.06, ALE–PLE: 0.01; tapeta outlines visible but no longer reflective. Legs: I: 4.42, II: 4.00, III: 2.06, IV: 2.50; anterior femurs with one or more dorsolateral macrosetae distally, not strongly developed. Abdomen: length 1.34, width 0.82; similar to *D. incanescens* male but square anteriorly. Palpal organ (Figs 64, 65): palpal femur 0.28× carapace length; patella without macroseta, tibia c. 1.5× as long as wide; embolus tapering with distinct process at c. 1/3 distance to tip (arrowed in Fig. 65); embolic apophysis a broad slightly kinked strap, widening to a paddle shape at c. ½ length; bulbus elongate, width: length = 1:2.0. Colour in alcohol: traces of black on lateral carapace and around and behind PME; abdomen with traces of black in similar pattern to female except for extra row of dark spots down midline in posterior half.

Female (holotype). Carapace (Fig. 66): length 1.47 (range 1.29–1.47), width 1.18, height 0.61; humped, but like in male rather lower than other species, broad in dorsal view. Chelicerae: 2 promarginal teeth plus large intermediate, retromarginal cheliceral teeth not visible due to tightly closed position of chelicerae against mouthparts. Labium: anterior not visible. Sternum: gently convex, but less so than small species. Eyes (Fig. 66). AME: 0.15, PME: 0.10, ALE: 0.10, PLE: 0.09, AME–AME: 0.035, AME–ALE: 0.05, PME–PME: 0.04, PME–PLE: 0.10, ALE–PLE: 0.035; no reflective tapeta visible. Legs: I: 5.94, II: 5.08, III: 2.78, IV: 3.55. Only one macroseta visible on distal retrodorsal femurs of legs I, II and IV, none visible on femur III. Abdomen (Figs 67, 68) (separated from prosoma): length 3.18, width 1.96. Broadly bilobed, lobes barely developed vertically, so appears almost square-topped; post genital mound barely developed. Epigyne (Figs 69, 70): copulatory openings of epigynum set away from posterior margin in ventral view, epigynum medially broad with marginal sculpturing, lateral lobes obvious and lightly sclerotized; internal margins of the lateral plates broadly separated and shallow in posterior view. Internal genitalia (Fig. 71): copulatory ducts pass spermathecae medially, entering lower lobe posteriorly; spermathecae apparently bilobed, lobes connected by bulging duct-like section; head more or less globular. Colour in alcohol: carapace creamy-white, region of PME and area immediately posterior brown, brown patches on sides of caput and carapace; sternum with brown mark posteriorly. Legs faintly annulated with brown; tarsi paler. Abdomen dorsum pale except for brown patch anterior to anal tubercle and remains of paired markings towards anterior; brown lateral patches; ventrally with olive-brown over post-genital mound, outlined with white lines.

Distribution. *Dolichognatha raveni* has been recorded from the type locality in the Iron Range on Cape York, north-eastern Australia and from eastern Papua New Guinea.



FIGURES 61–71. *Dolichognatha raveni*. 61–65, male (QM S78041). 61, eye region and chelicerae, frontal (slight rotation); blunt cheliceral tooth near fang tip arrowed. 62, eye region and chelicerae, lateral; arrow indicates anterolateral carapace projection. 63, right maxillary endite and labium, frontal. 64, 65, male palpal organ, ventral, retrolateral; arrow indicates embolic process. 66–71, female (holotype). 66, carapace, dorsal. 67, 68, abdomen lateral, dorsal. 69, 70, epigynum, ventral, posterior. 71, epigynum dorsal (internal genitalia). Scale lines 0.5 mm for somatic parts, 0.1 mm for genitalia.



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FIGURE 72. Consensus tree for the tetragnathids. The unfigured part of the tree remains as in the original study (Hormiga *et al.* 1995). Unambiguous character changes shown, filled squares = non-homoplasious; open squares = homoplasious. Number above symbol is the character number; number below is character state.

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Appendix. *Dolichognatha* specimens examined as part of this study (and not detailed in text).

Repository & reg. no.	Sex	Data	Notes
AM KS57548	1 ♀	USA: S.C. Oconee County, Chattooga R., 1.5 mi S Russell Brudge (sic) on Rt 28, 1580 ft elevation, 18 July 1998.	Det. <i>Dolichognatha pentagona</i> , M. Kuntner 2002. No reflective tapeta visible.
AM KS59040	1 ♂ 1 ♀	Australia: Western Australia, Cave Springs NNE of Kununurra, 29 May 1999, Gray, Milledge & Smith: in web on cave wall.	<i>Dolichognatha</i> sp. (s.str.) Four abdominal humps. No reflective tapeta visible. Male labral spur not obvious, if present folded flat.
BMNH	2 ♂	Sulawesi: Utara, Dumoga, Nov. 1985, P. Hillyard.	<i>Dolichognatha</i> sp. Four abdominal humps. Extremely elongate chelicerae, modified distally. Clearly visible reflective tapetum in PME (condition in other eyes not noted).
QM S30829 – S30837	2 ♂ 10 ♀ jj	Fiji: various localities, G. Monteith <i>et al.</i> , June–July 1987. Most “pyrethrum/ logs & trees”.	<i>Dolichognatha</i> sp. (s.str.) No reflective tapetum visible on any specimen. All Fiji specimens appear to belong to the same species. Males have labral spur.
QM S13535	1 ♂	Fiji: Nananu-i-ra Island, Vitu Levu, <i>Pisonia</i> , fig tree shoreline forest 24.xi.1988, T.B. Churchill.	
QM S74355	1 ♂	Australia: Queensland: Homevale, MEQ (10), RK, VED, 1–7.iv.1975, horizontal orb web.	<i>Dolichognatha</i> sp. (s.str.) Condition not good enough to assess tapeta. Labral spur not obvious, if present folded flat.
RMNH ex coll. CLD	2 ♀	Indonesia: Kalimantan: Kaharian, 2–16.ix.85, Suh. Djojosudarmo, swampy primary forest, foliage.	<i>Dolichognatha</i> sp. Abdomen ovoid, no humps, pedicel closer to apex than spinnerets; reflective tapeta in all secondary eyes; femora with few macrosetae, lower legs with many; carapace short.